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¿Arthropoda?   **PENTASTOMIDA**   **Manual**

Versión española

Pentastomida

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1. Brief characterization of the group and main diagnostic characters

1.1. Introduction

Pentastomids are elongated, flattened or cylindrical. The bilaterally symmetrical body is divided into a **cephalothorax** and a **trunk** region. There is little resemblance to arthropods except in the mite-like shape of the larva (Mapp *et al.*, 1976). This primary larva invades the gut of the host using the **penetrating apparatus** (Self, 1969).

The larvae have a ventral mouth and two pairs of hooks (Abadi *et al*, 1996), with little resemblance to the free-living nauplius larvae of crustaceans. Adult pentastomid species are easily distinguished from any other parasite by the two pairs of **retractile hooks** on either side of the mouth (Paré, 2008). These hooks are used to anchor the animal to the host tissues (Riley, 1986). The cuticle is **chitinous** and porous, being **moulted** occasionally. The mouth lacks jaws. The gut is strait and ends in a posterior anus. Longitudinal and circular muscles are cross-striated. The nerve chord is ventral and ganglionated. Fertilization is internal. Excretory and respiratory systems are absent.

Recent pentastomids are parasites of tetrapods and predominate in the tropics and subtropics (Self, 1969). *Reighardia sternae*, with its monoxenous development (with no intermediate hosts), has conquered polar and subpolar latitudes in the Holarctic region (Nicoli & Nicoli, 1966). *Linguatula serrata* (Fröhlich, 1789), with a life cycle restricted to mammals, has become cosmopolitan.

Fossil pentastomids occur in Cambrian and Ordovician marine strata of Sweden and Canada, being older than all known arthropod parasites. They differ from Recent forms most markedly by the presence of two additional pairs of somites with appendages in front of the genital pores (Waloszek & Müller, 1994).

1.2. Morphology

The cephalothorax may bear two pairs of anterior **sensory papilla**. The trunk is finely annulated, and may be worm-shaped or dorsoventrally flattened (the reason for the alternative group name Linguatulida, or tong worms). A terminal or subterminal **anus** may be flanked by a pair of **terminal papillae** (Haffner, 1977).

The **cuticle** is chitinous, similar to that of arthropods, but simpler (Trainer *et al.*, 1975). This chitin is of the plesiomorphic β-form as present in Cnidaria, Annelida, Mollusca, and Brachiopoda. Arthropods

possess the more apomorphic α -chitin (Dennell, 1960). Furthermore, the cuticle is soft enough to allow **peristaltic locomotion** (Riley & Banaja, 1975). Internal organs are suspended in **haemolymph** (Parré, 2008), which is contained in a **haemocoel**. Muscles are arranged into **longitudinal and circular layers**, as in annelids (Doucet, 1965). But while these muscles are obliquely-striated in annelids (Mill & Kapp, 1970), in pentastomids they are **cross-striated**, as in arthropods (Storch, 1993). A variable number of **moults** occur in development (Buckle *et al.*, 1997). **Sensory organs** are reduced to **dorsal lobes**, and apical, terminal and **frontal papillae** on the cephalothorax (Böckeler, 1982). At least two pairs of these sensory papillae may correspond to **reduced appendages** (Riley, 1986). The trunk may contain minute annular **pores**, sometimes regularly arranged, which may represent the openings of certain epidermal glands (Riley, 1973). **Sensory cells** associated with the **lateral line system** may be osmo- or chemosensory in function (Ali & Riley, 1985). Mechanosensitive **sensilla** located on the dorsal and frontal papillae may have a tactile function and may be important in orientation (Ali & Riley, 1985). They show a close correspondence to the sensilla of arthropods (Storch, 1979).

The **nervous system** is very similar to that of arthropods, with a supraoesophageal portion forming the brain and a subesophageal ganglionated nervous mass (Doucet, 1965). The **cerebral mass** has two pairs of **ganglions**, the anterior ones enervating the sensory organs and the anterior head muscles; the second pair of ganglia (apparently representing the tritocerebrum) ennervate the buccal region and sensory papillae near the first pair of hooks. The third pair of ganglia is ventral and innervates the first pair of hooks. The fourth pair of ganglia innervates the second pair of hooks. The fifth to seventh pairs of ganglia innervate different portions of the genital organs. The eighth pair gives rise to posterior nerve chords that extend to the posterior of the trunk (Böckeler, 1984a). This basic disposition may become modified in some groups (Osche, 1963).

The **digestive tract** is straight, tubular, ending in a posterior **rectum** or **cloaca**. The **mouth** is sustained by a **chitinous buccal ring**. The pharynx is delimited by two **chitinous plates** and functions as a **pharyngeal pump**. An **oesophagus** extends to the **middle intestine**, from which it is separated by a **valve**. The **pyloric valve** leads to a short **posterior intestine**, which ends in the **anus**. The entire course of the intestine is chitinized. Various **glands** discharge into the buccal cavity and into the middle intestine (Legendre, 1967). Clitellate-like **cloragogen glands** are also associated with the digestive tract. Both adults and larval forms are haematophagous (Riley, 1986). Unlike arthropods, they have no piercing, biting or sucking extremities. They rely on a sucking mechanism provided by two rigid plates located in the pharynx and several associated muscles (Thomas & Böckeler, 1992a, b). Digestion is mostly **extracellular** (Thomas *et al.*, 1999a, b).

Pentastomes are **dioecious** and sexually dimorphic (Junker, 2002). Egg-production is massive (Riley, 1983). Copulation occurs only one in the lifetime of a female (Storch *et al.*, 1990). Sperm becomes permanently stored in the **spermathecae** (Riley, 1983). Genital organs are initially paired, but become secondarily fused, being located along the dorsal length of the trunk. The **genital pore** of the male is anterior in position, flanked by the peribuccal papillae (Hett, 1924). The male genital system consists of an unpaired testis and an unpaired (Cephalobaenida) or paired (Raillietiellida) **seminal vesicles**, leading into the **vasa deferentia**. The **ejaculatory ducts** open into the vasa deferentia, at the junction with the seminal vesicles. **Cirri** are extremely long, coiled tubes located within a spacious **cirrus sac** (Storch *et al.*, 1990). **Sperm** develops in an unpaired **testis**, and is released into the seminal vesicles. Sperm becomes retained there until **copulation**. From there they are released into the **ejaculatory bulbs**. These reach the vasa deferentia, which merge with a **dilatator**, losing their epithelium and becoming **cuticular tubes**. The dilatator guides the cirrus into the genital tract of the female. The male **genital atrium** may be further extended into a **copulatory organ**, enabling the cuticular tubes to penetrate the female openings (Böckeler & Storch, 1990).

The female reproductive system is complex. The **ovary** may be divided anteriorly or posteriorly (Nørrevang, 1972), which indicates that if was originally a paired organ (Nørrevang, 1983). The haemocoel of mature females is occupied by the **uterus**, containing eggs in various stages of development (Riley, 1986). Paired **spermathecae** are found at the junction between the **oviduct** with the uterus. Because the uterus expands enormously during development, the spermathecae become increasingly removed from the **vagina** (Riley, 1986), in contrast to arthropods, where both structures remain close (Chapman, 1971). The single insemination occurs in young females, before the development of the uterus (Ali & Riley, 1983). Spermathecae not only store sperm, but provide continuous **fertilization of oocytes** (Riley, 1986). The vagina stores eggs before release and sieves for egg size (Riley, 1986).

1.3. Development

Development ranges from indirect, with up to 10 successive nymphal (or larval) stages, to direct. Larvae hatch with **seven pairs of somites** (Riley, 1986). Embryonic development ends with a pre-hatchling within the eggshell, the so-called **primary larva** or nymph. The **hatching larva** acquires mobility, frontal papillae, and a **chitinous rod** to penetrate the host´s gut (Storch & Böckeler, 1982). The larvae then migrate through the body cavity. After several moults, the **infective larva** attains maturity in the respiratory tract of the definitive host (Buckle *et al.*, 1997).

Embryonic development occurs within a series of **egg membranes** (Riley, 1986), which are secreted by a glandular **dorsal organ** (Osche, 1963). According to Stendler-Seidel *et al.* (1997a), this structure is not homologous to the dorsal organ of arthropods. Larvae hatch with four head segments and three trunk segments, and two more body segments are added during postembryonic development (Böckeler, 1984a). Thus larvae and adults possess the same number of body segments (Waloszek & Müller, 1994). Later

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stages do not develop additional trunk segments (Castellani *et al.*, 2011). Segmentation is of the **spiral** type (Osche, 1963; Doucet, 1965). The primary coelom does not persist to the adult stage, being replaced by a myxocoel (Legendre, 1967). Hatched eggs represent the infective stage for the next hosts in the life cycle (Riley, 1986), but the details of these life cycles vary among the different groups of pentastomes.

1.4. Life cycle

The **life cycle** is adapted to to an obligate endoparasitic lifestyle in the respiratory tracts of vertbrates (Paré, 2008). Most species are tightly host-specific (Riley, 1986). Reptiles represent the mains hosts. An **intermediate host** is one in which the primary larva develops to the infective stage. A **definitive host** is that in which parasites must be capable of attaining sexual maturity (Fain, 1964). **Larvae** are found free in the body cavity or encapsulated in the digestive tract tissues and associated organs or in muscles and mesenteries close to the alimentary tract (Shipley, 1898). Most pentastomids have two successive hosts. Some have a direct cycle, others may have two or more intermediate hosts (insects, fish, amphibians, reptiles, or mammals) (Sambon, 1922), either aquatic or terrestrial (Banaja *et al.*, 1975). Riley *et al.* (1978) hypothesized that the ancestral pentastomid was originally a parasite of fish and only subsequently became adapted to aquatic reptiles when fish were predated by the latter (Olson & Cosgrove, 1982). Adult parasites from the respiratory tracts of the definitive hosts release their eggs into the lungs and nasopharynx, gaining access to the esophagus. Eggs, normally deposited in the feces, become immediately infective and contain primary larvae that specialize in tissue migration (Self, 1969). The larvae have two pairs of legs with **double hooks**, as well as **penetration spines** and **stylets** on the dorsal cephalothorax enabling it to penetrate and transpose tissues (Keegan, 1943). Development to the adult occurs without **true metamorphosis**, but a series of **larval instars** are present, each separated by a **moult.** The life cycle is completed when an infected intermediate host is consumed by the definitive host (Riley, 1993).

1.5. Ecology

As parasites, pentastomids are regulators of host populations. Pentastomids are often recovered from autopsies in zoo animals. In Australia, they have been linked to health problems in crocodiles reared in farms and parks (Junker, 2002). From a conservaton point of view, it will be important to determine how pentastomids affect and regulate rare and endangered host species (Riley, 1986). Pentastomids may also represent a health problem for man in certain regions of the world, particularly Africa, The Middle East, South-East Asia (Riley, 1986) and Latin America. They strive in poverty-stricken communities living in arid regions, where subsistence feeding on native reptiles may facilitate transmission of infective nymphs (Almeida & Christoffersen, 2002).

Adult Pentastomida are restricted to the respiratory tracts of tetrapods, mostly reptiles (Thomas & Böckeler, 1992a). Only larval stages, however, may occur in fish. Paleozoic forms are exclusively marine. Unlike other mandibulate parasites, they lack modified mouthparts for piercing capillaries (Thomas & Böckeler, 1992a). Species of Pentastomida causes visceral and respiratory pentastomiasis in vertebrates, including man, and may have an ecological role as regulators of the size of communities.

1.6. Taxonomy

The identification of pentastome parasites is based on relatively few morphological characters (Riley, 1986). Because males are usually short-lived, mostly female are used in species diagnosis. The male copulatory spicule becomes important in specific diagnosis only in raillietiellids (Ali *et al.*, 1985). Classification is based mainly on mouth and hook position and shape, presence of glands, and morphology of genitalia (Riley, 1969; Paré, 2008). Unfortunately these characters are subject to a high level of intraspecific variation. For example, hooks increase in size and may change in shape at each moult (Fain, 1964). Body size may be influenced by host (Giglioli, 1927) and number of annuli are known to vary intraspecifically (Ali *et al.*, 1982, 1984). For the identification of species of larvae causing visceral pentastomiasis, molecular diagnostic methods have become necessary (Mätz-Rensing *et al.*, 2012).

1.7. Diseases caused by pentastomes

Pentastomiasis may be of two types:

a) Visceral pentastomiasis (caused by the larva).
Nymphs installed in the intermediate hosts produce granulations in viscera and infected tissues, causing mechanical tissue damage and hemorrhage (Boyce & Kazacos, 1991). Visceral pentastomiasis is a common disease in many tetrapods, mostly reptiles, but also affecting man.

b) Respiratory pentastomiasis (caused by adults).
Adults live in the respiratory tracts (nasal airways, frontal sinuses, and tympanic cavity) of the definitive host. Respiratory pentastomiasis causes hemorrages and breathing difficulties (Bowman, 2000; Alcala-Canto *et al.*, 2007). Only *Linguatula serrata* is known to infect the respiratory tracts of man (Riley, 1986).
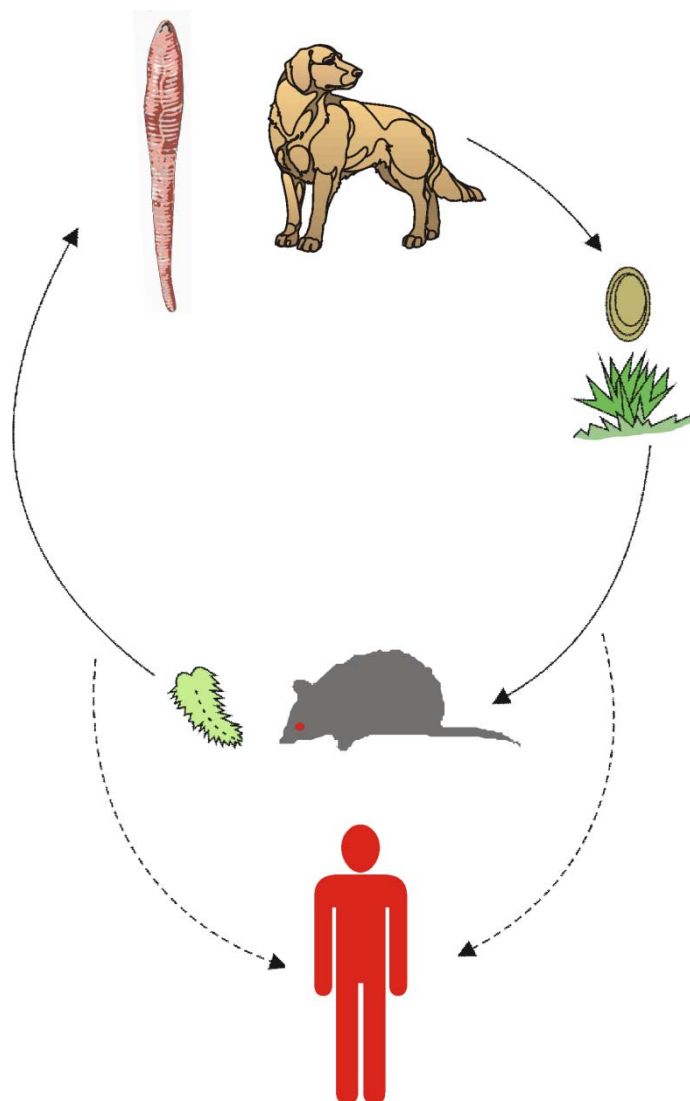
Fig.1. Life cycle of *Linguatula serrata*, asso-ciated to different stages of pentastomiasis (adapted from Arroyo *et al*., 1986).

2. Systematics of the group

Historically pentastomids have been allied to arachnids (Acari), crustaceans (Branchyura) and myriapods. However, they do not share convincing apomorphies with any of these arthropod groups. A phylogenetic system for the Pentastomida was proposed by Christoffersen & De Assis (2013) (Table I).

Table I. System of the Pentastomida. SOURCE OF DATA: Christoffersen & De Assis (2013).

Phylum Pentastomida Huxley, 1869 (29 gen., 8 spp fósiles, 144 spp-ssp actuales)
    Pan-Pentastomida [clado ancestral (stem-group) + clado actual (crown-group)]
    Clado ancestral de pentastómidos (4 gen. fósiles, 8 spp. fósiles)
    Clase Eupentastomida Waloszek, Repetski & Maas, 2006 (clado actual, 25 gen. actuales, 144 spp. actuales)
      Orden Cephalobaenida Heymons, 1935 (2 gen., 2 spp)
        Familia Cephalobaenidae Heymons, 1922 (2 gen., 2 spp)
      Orden Raillietiellida Almeida & Christoffersen, 1999 (2 gen., 44 spp-ssp)
        Familia Raillietiellidae Sambon, 1922 (2 gen., 44 spp and ssp)
      Orden Reighardiida Almeida & Christoffersen, 1999 (2 gen., 3 spp)
        Familia Reighardiidae Heymons & Vitzhum, 1936 (2 gen., 3 spp)
      Orden Porocephalida Heymons, 1935 (19 gen., 95 spp-ssp)
        Superfamilia Linguatuloidea Haldeman, 1851 (3 gen., 10 spp-ssp)
        Familia Linguatulidae Leuckart, 1860a (2 gen., 6 spp-ssp)
        Familia Subtriquetridae Fain, 1961 (1 gen., 4 spp)
      Superfamilia Porocephaloidea Sambon, 1922 (16 gen., 85 spp-ssp)
        Familia Sebekiidae Sambon, 1922 (8 gen., 41 spp)
          Subfamilia Leiperiinae Christoffersen & De Assis (2013) (1 gen., 3 spp)
          Subfamilia Samboninae Heymons, 1935 (1 gen., 5 spp)
          Subfamilia Diesingiinae Heymonss, 1935 (3 gen., 13 spp)
          Subfamilia Sebekiinae Sambon, 1922 (3 gen., 17 spp)
        Familia Porocephalidae Sambon, 1922 (8 gen., 44spp-ssp)
          Subfamilia Armilliferinae Kishida, 1928 (2 gen., 13 spp-ssp)
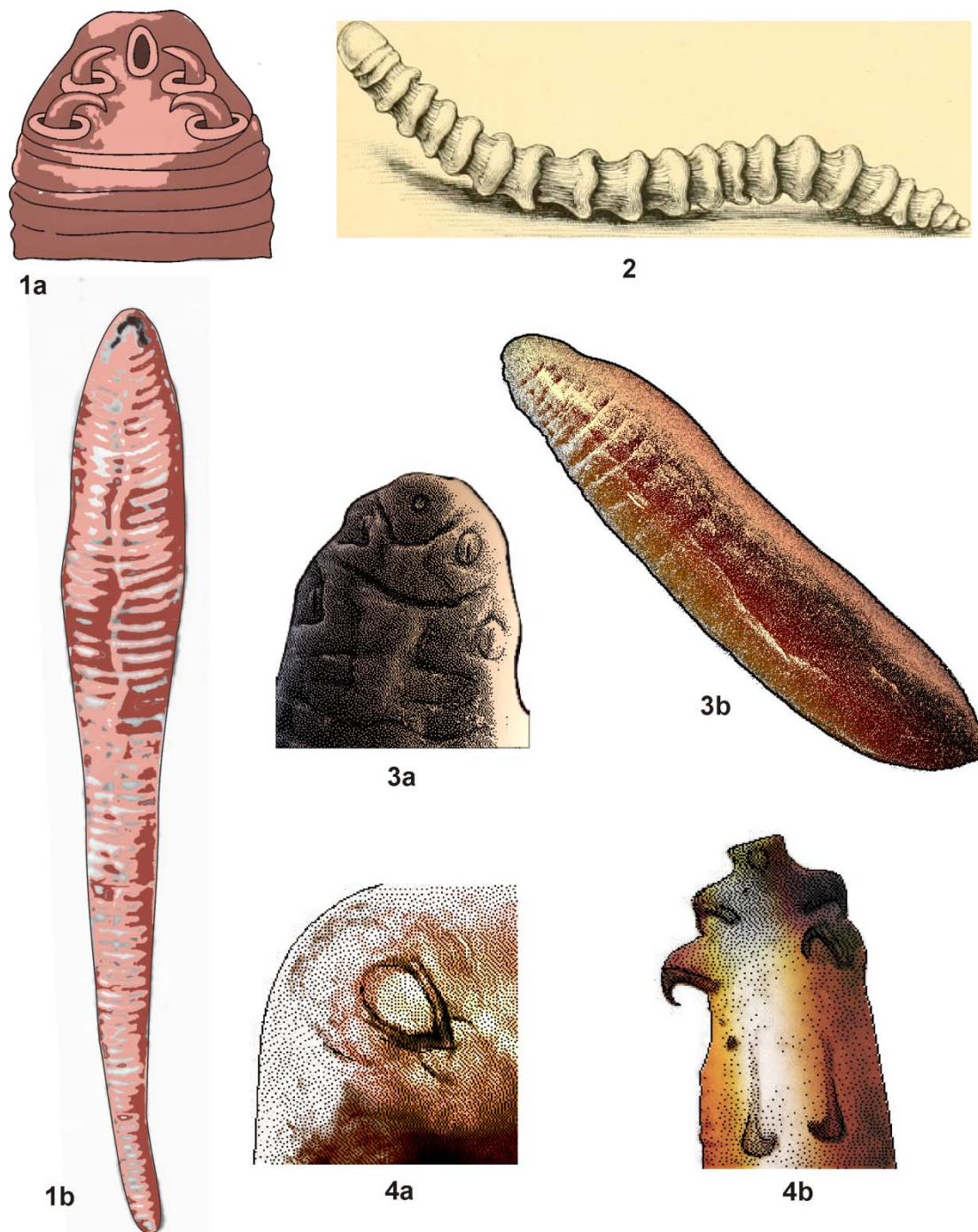   Subfamilia Porocephalinae Sambon, 1922 (6 gen., 31 spp)

Lámina I: 1. *Linguatula serrata* (Fröhlich, 1789): **1a**) Cabeza; **1b**) Aspecto hembra adulta. **2**. *Armillifer armillatus* (Wyman, 1848). **3**. *Hispania vulturis* Martínez, Criado-Fornelio, Lanzarot, Fernández-García, Rodríguez-Caabeiro & Merino, 2004. Dibujos a partir de fotografias: **3a**) Región anterior; **3b**) Aspecto general. **4**. *Raillietiella morenoi* Abreu-Acosta, Rodríguez Foronda, Valla-dares & Casanova 2006, dibujos a partir de fotografias: **4a**) Boca y faringe (hembra); **4b**) Cabeza (macho).

3. Diversity of the group

There are only 144 Recent and 8 fossil species of Pentastomida known worldwide. Despite their low diversity, pentastomids occur globally, are common parasites of the respiratory tract of vertebrates, particularly reptiles, and produce visceral and bronchial linguatulosis which occasionally affects man.

Only four species have been cited for the Iberian Peninsula and Macaronesian Islands:

1) ***Railietiella morenoi*** Abreu-Acosta, Foronda, Rodríguez, Valladares & Casanova, 2006, described as new from adults parasitizing the lungs of an endemic lizard in the Canary Islands (Abreu-Acosta *et al.*, 2006). *Raillietiella* belongs to the second most primitive clade of pentastomids (Raillietiellida, see Almeida & Christoffersen, 1999). It is relatively diverse (43 species), being found in all regions of the world. This contrasts to the most basal clade (Caephalobaenida), which is restricted to South America.

2) ***Hispania vulturis*** Martínez, Criado-Fornelio, Lanzarot, Fernández-Garcia, Rodríguez-Caabeiro & Merino, 2004 ocurs in the abdominal air sacs of the black vulture, *Aegypius monarchus* (Linnaeus, 1766) from Spain (Martínez *et al.*, 2004). This new species is the third species known to parasite the lungs of birds as adults. The first two belong to the genus *Reighardia,* being restricted to marine birds. *Hispania* forms the sister group to this genus, being now placed within the Reighardiidae, belonging to the monotypic order Reighardiida (Almeida & Christoffersen, 1999).

There are two further reports of pentastomids from birds (*Anthropoides virgo* and *Porphyrio* sp.), but in this case the birds are acting as intermediate hosts (for the pentastome *Cubirea annulatus*), probably as a consequence of the birds having eaten an infective snake (Riley, 1986). The description of *Hispania vulturis*, however, is based on immature specimens and there is need for more detailed morphological information and illustrations of this interesting Spanish taxon.

3) ***Linguatula serrata*** was collected from the hare *Lepus granatensis* in Spain (Moreno Montanéz *et al.*, 1979; Martinez-Gomez *et al.*, 1987). It was also found to be responsible for linguatulosis in a goat (Valero Lopez *et al.*,1980).

Linguatuala serrata is the only species known to infect man as adults, although respiratory pentastomiasis is rare in humans.

4) ***Armillifer armillatus*** (Wyman, 1848) was documented in a guinea pig from Portugal (Dias, 1942). The last two species cited above are responsible for most cases of visceral pentastomiasis worldwide, including Europe. Most reports are of accidental infections from man. These belong to the most apical order of pentastomids, the Porocephaloida. The two species belong to the sister-taxa Linguatuloidea and Porocephaloidea, respectively.

It so happens that the four identified Iberian species of Pentastomida (Table I) represent three out of the four present orders presently recognized within the phylogenetic system of the Recent Pentastomida (Christoffersen & De Assis, 2013). In *Armillifer* and *Linguatula* the definitive host is a carnivore such as a snake, and the intermediate host is a mammal (Fain, 1975).

The only other reference for pentastomids in the Balearic-Iberian-Macaronesian regions is the report of a case of pentastomiasis by an unidentified pentastomid in Madeira (Boavida, 1954).

The severity of human visceral pentastomiasis may vary, but this stage is usually asymptomatic; humans are usually highly tolerant to pentastomid infections (Abadi *et al.*, 1996). Although most visceral infections produce few or no symptons, severe infestations has caused intestinal obstruction, pneumoanitis, meningitis, pericarditis, nephritis, peritonitis, obstructive jaundice, and even death (Mapp *et al.*, 1976; Cagnard *et al.*, 1979). Pentastomiasis is usually discovered incidentally in an autopsy, a radiological examination, or during a surgical intervention (Abadi *et al.*, 1996).

Several species of pentastomes are known to produce visceral pentastomiasis in man, particularly in Africa (Ette *et al.*, 2003), Asia (Tappe & Büttner, 2009), and Latin America (Almeida & Christoffersen, 2002). Infections usually result from eating raw or insufficiently cooked reptiles. A nymph of *Leiperia cincinnalis* (which lives as adults in the lungs of African crocodiles) was found in the feces of a European woman in Zaire (Fain, 1960, 1961). This patient was probably infected by eating fish harboring the larvae (Fain, 1975).

Table II. Species of Iberian and Maccaronesian Pentastomida known in each area, with the system to which they belong. SOURCE OF DATA: Christoffersen & De Assis (2013).

Nº	Family	Species	Spain	Portugal	Canaries
1	Raillietiellidae	*Raillietiella morenoi*	–	–	+
2	Reighardiidae	*Hispania vulturis*	+	–	–
3	Porocephalidae	*Armilliffer armillatus*	–	+	–
4	Linguatulidae	*Linguatula serrata*	+	–	–

4. Current state of knowledge of the group

Pentastomida is an enigmatic group of arthropod-like parasitic worms, which lack arthropod apomorphies, and must thus be placed outside the Arthropoda proper, like other smaller phyla such as the Onychophora, Tardigrada, and Myzostomida. They are not crustaceans, because their limbs are not organized into a proximal basipodite from which two rami (endopodite and exopodite) arise. Nor do they have free-swimming larvae, such as the nauplius and zoeae in crustacean. They are also not euarthropods because they lack a segmented antenna on the head. Almeida *et al.* (2008) placed them in the ecdysozoan taxon Mysopharyngea, together with Tardigrada and Nemathelminthes. Evidence from sperm ultrastructure and molecular data has placed them as degenerate branchyuran crustaceans. But the absence of mandibulate morphological apomorphies, and the much older (Cambrian) age of Pentastomida, are counter to this hypothesis.

The following apomorphies place Pentastomida within the Ecdysozoa: (**1**) the presence of a hemocoel (sometimes referred to as a pseudocoel or myxocoel); (**2**) the presence of ß-chitin in the cuticle (Karappaswamy, 1977); (**3**) hooks of the penetrating apparatus are cuticularized; (**4**) the anterior and posterior digestive tract is chitinized (also in Tardigrada); (**5**) ecdysis is present, probably controlled by hormones; (**6**) free cilia are absent.

5. Main available source of information

General overviews of the Pentastomida were provided by Heymons (1935), Hill (1948), Self (1969), Poore (2012) and Christoffersen & De Assis (2013).

The first phylogenetic system of the Pentastomida is provided by Almeida & Christoffersen (1999), being supplemented with a phylogeny of the Sebekiidae (Junker, 2002, unfortunately still not published). Recent advances on the phylogenetic system of the Pentastomida were given in Christoffersen & De Assis (2013).

Advances in morphology are Böckeler (1980, 1984a, b), Böckeler & Storch (1990), Stender-Seidel & Gabrielle (1997), Stendel-Seidel *et al.* (1997a, b, 1999, 2000), Storch (1984, 1993), Storch & Böckeler (1979, 1982), Storch *et al.* (1990), Thomas (1965), Thomas & Böckeler (1992a, b, 1994), Thomas & Stendel-Seidel (1996), and Thomas *et al.*, 1999a, b, c) for extant species, and Waloszek & Müller (1993, 1994) and Waloszek *et al.* (1994, 2006) for fossil species.

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